SOLIVA (ASTERACEAE: ANTHEMIDEAE) IN CALIFORNIA

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ABSTRACT

Soliva sessilis, S. pterosperma, and *S. daucifolia* have been distinguished from each other on achenal characteristics and habitat, and have been listed as members of the naturalized flora of California. Examination of over 310 collections from California documented a continuum of achene morphology and an indiscriminate distribution of morphs that form a single taxonomic species. Synonymy of *S. sessilis* also is extended to include *S. neglecta* and *S. valdiviana.*

Soliva Ruiz Lopez & Pavon is a genus of low growing annuals first described in 1794 from Chile. Native to South America, it was naturalized in California by 1836 when Nuttall visited Santa Barbara and collected what he later (1841) described as *S. daucifolia. Soliva* may have come to California from Chile in shipments of hides (Cabrera 1949, Healy 1953), but probably not on livestock (Raven 1963).

Achenes of *Soliva* are well adapted for long-distance dispersal, as suggested by their unique morphology. They are small and lightweight with stiff, appressed pubescence, and disperse by adhering to animals or other objects that move. More importantly, however, they have a sharp, persistent stylar spine that easily becomes imbedded in dispersal agents. *Soliva* is found most often in hard-packed soil or near well-beaten paths or roadsides. In addition, it is found in planted lawns. Human activities are probably a major means of dispersal for *Soliva,* which occurs mainly in areas with large human populations or along major travel routes. *Soliva* spp. are adventive and have become established world-wide in many such locations.

Soliva sessilis, S. pterosperma, and *S. daucifolia* have been recognized for California (Crampton 1954), although two other species, *S. neglecta* and *S. valdiviana,* could be recognized based on published descriptions by Cabrera (1949) and Philippi (1864–65). This group of species was called subgenus *Eusoliva* (=*Soliva*; see Voss et al. 1983) by Cabrera (1949) and includes about half of the genus. The remaining five species do not occur in North America and differ markedly from the species considered here in both achene and vegetative characters (Cabrera 1949). Cabrera (1949) treated *S. daucifolia* as a synonym of *S. sessilis,* and distinguished between it and the remaining species only by means of achene characters. Crampton

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(1954) distinguished between *S. sessilis, S. pterosperma,* and *S. daucifolia* by achene characters and habitat. All published descriptions for the five taxa are basically identical with regard to vegetative and floral morphology; both kinds of characters are deemphasized because they are not used to distinguish the species. Floral morphology is of limited use as a descriptive or distinguishing character because of the short duration and minute size of the flowers.

The generally accepted (Cabrera 1949, Crampton 1954, Munz 1959) achene morphologies that characterize the five taxa under discussion are illustrated in Fig. 1 (A–E). Achenes of *S. sessilis* are pubescent and have wide, entire wings that usually have large wing-tips. Achenes of *S. pterosperma* are pubescent and have wide wings, long, tapering, curved tips, and a large sinus between upper and lower wing-lobes that is positioned about one-third of the distance from the base to the top of the wing (excluding the wing-tip). Achenes of *S. daucifolia* are pubescent, have no wings, but have small wing-tips. Those of *S. neglecta* are similar to those of *S. sessilis,* except they are glabrous rather than pubescent. *Soliva valdiviana* usually includes plants with wingless, wing-tipless, glabrous achenes (Cabrera 1949), but Philippi's (1864–65) original description does not specifically mention a lack of pubescence and refers to the presence of wing-tips. Notes on many specimens of *Soliva* suggest that the achene characters are unreliable. This paper presents an examination of *Soliva* collections from California to determine the species present, and a study of achene and general morphology to review the distinguishing characteristics for the species considered.

Materials and Methods

To examine achene and vegetative morphology and determine which species of *Soliva* occur in California, I studied over 250 specimens from CAS, CHSC, DS, JEPS, POM, RSA, and UC. I also made 60 collections of *Soliva* in various parts of the state. A list of specimens examined in this study is included in Ray (1984), which is available at Stanford University and CAS.

Some terms used in this paper relative to achene morphology are illustrated in Fig. 1 (F–R). Wing-tips are usually pointed projections that occur in pairs on either side of the central stylar spine (see Fig. 1 and below), and often the outside edges are continuous with those of the wing. The wing is a region flattened in the plane of the achene that occurs on either side of the achene. The stylar spine, derived from the persistent style, arises from the center of the achene and is continuous with the central, thicker body of the achene. A sinus is a region where the edge contour of the wing is broken sharply, like a "bite" out of the wing, or sometimes appears as a crack. An incurved region of the wing is a kind of sinus with a very

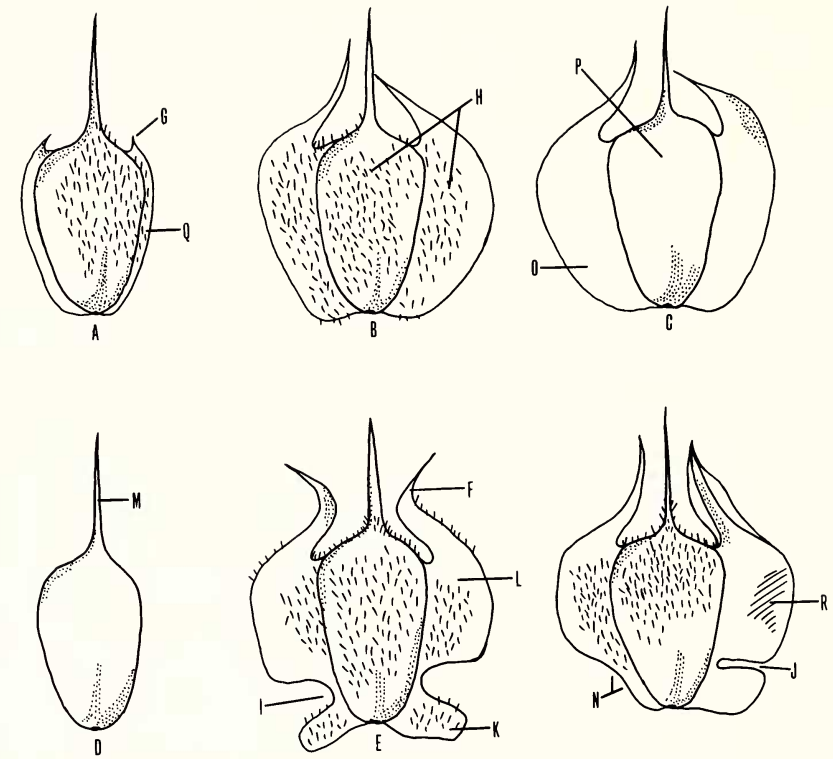


FIG. 1. Achene morphologies for five "taxa" of *Soliva* (after Cabrera 1949, Crampton 1954). A. *S. daucifolia.* B. *S. sessilis.* C. *S. neglecta.* D. *S. valdiviana.* E. *S. pterosperma.* Morphological terms used in the text: F. Long wing-tip. G. Short wing-tip. H. Typical short, stiff, appressed pubescence on achene "body" and wings. I. Sinus. J. Narrow sinus. K. "Below" (lower lobe). L. "Above". M. Stylar spine. N. Incurved region of wing. O. Wing entire. P. Achene "body" (in this case glabrous). Q. Narrow wing (=margin). R. Hyaline area of wing (thin and transparent).

shallow, smooth interruption of the wing edge contour.

Although vegetative morphology has not been used in the literature to distinguish the species of *Soliva* under consideration here, I examined vegetative characters in view of possible relationships to achene characters. These characters included typical habit and size of plants; leaf position, shape, divisions, surface texture, and pubescence; internode characters; and aspects of the inflorescence.

I examined achenes from each collection by stereoscope. One or more (depending on variation occurring on sheet) representative achenes were drawn in detail and described. Achene body and total length were measured, because this character has been used to recognize *S. daucifolia* (Crampton 1954). Vegetative characteristics from

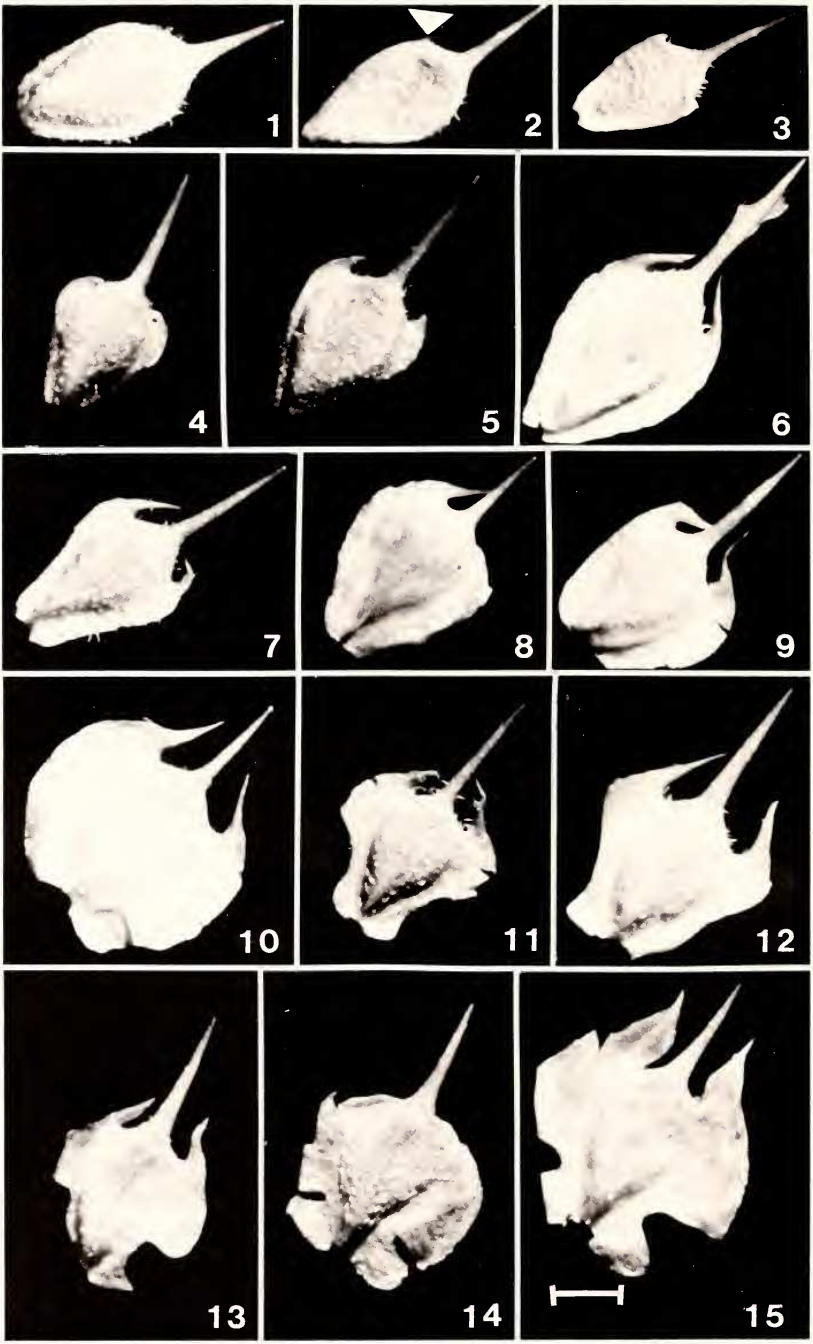
each collection were described. Based on the accumulated data, 15 achene morphology categories (Fig. 2) were designated, each represented by a specimen. I then assigned all specimens to one or more (depending on variation) of these morphological categories.

The range of *Soliva* achene variation is described here by reference to the above mentioned series of 15 numbered, artificial achene morphs. The features of each morph are described in detail in the caption for Fig. 2. Although the artificial morphs are discrete, many further intermediates occur, and in fact every achene is somewhat unique. The morphs are not necessarily spaced equally over the range of variation. Some morphs are of more general form than others, and thus contain more internal variation (intermediates) and represent more collections. Achene morphology was not always uniform in a particular collection and I noted many cases in which variation occurred on individual plants or even within capitulae. The generally recognized species (Cabrera 1949, Crampton 1954) correspond approximately with the artificial achene morphs (Fig. 2) as follows: *S. valdiviana,* morphs 1–2; *S. daucifolia,* morphs 4–6; *S. sessilis,* morphs 9–10; and *S. pterosperma,* morphs 13–15. *Soliva neglecta* is found among *S. sessilis* morphs. In the following text, the phrase "achene morph" or "achene morph number" refers to an actual observed morphology corresponding to that particular numbered artificial morph from Fig. 2.

Results and Discussion

Achene morphology. Achenes in all specimens have a central portion or "body" of more or less similar shape, including a sharp, persistent stylar spine (Fig. 1P), and most also have wings of various shapes and sizes, and/or wing-tips. A few achenes are wingless and wing-tipless. A carina on the achene body toward the base on the convex (abaxial) side is usually more pronounced in the drier collections from late in the season. Achenes and their appendages vary in color from light green or tan to dark brown. They vary in the distribution of typically short, stiff, appressed pubescence, and often have minute purple spots variously distributed on the body, stylar spine, and wings. The achene body is usually bilaterally symmetrical, but the two wings and wing-tips sometimes differ from one another in shape and size. Wings vary in shape, width, thickness, and edge characters, such as splits, cracks, and sinuses. Some wings are translucent or hyaline in limited regions. Wing-tips vary in width, length, curvature, and degree of furcation (Figs. 1, 2). Wing-tips on a given achene are sometimes dissimilar.

Total achene length varies from 3.5–5.2 mm. Crampton (1954) reported that *S. daucifolia* had achenes with consistently shorter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bodies than those of either *S. sessilis* or *S. pterosperma.* I observed no consistent relationship between achene body length and a particular achene morphology. Achene body length appeared to vary with overall length.

I observed no consistent relationship of any vegetative character or group of such characters to any achene character. In fact, vegetative morphology was relatively uniform in all specimens. Some previously unreported minor details of habit and leaf morphology were observed, and I have included these in the description below (compare with Cabrera 1949, Munz 1959).

A number of specimens that I examined corresponded with the description (with illustration) of *S. neglecta* Cabrera [e.g., *Bacigalupi 1527* (DS), *Breedlove 4405* (DS), *Cerrate 2515* (UC), *Eastwood and Howell 2561* (CAS), *Knight 626* (CAS), *Mason 4315* (DS), and *Raven 19734* (DS, RSA)]. Achenes from these specimens also usually matched the generalized morphology of *S. sessilis* (Fig. 1), but are glabrous or nearly so. This condition also was found in other col-

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FIG. 2. Achene variation in *Soliva sessilis.* Achenes shown are from representative collections that are cited below and that form the basis for artificial achene morphs, which describe the range of wing and wing-tip variation. Morphs are numbered 1–15, and are followed by a description and citation. Compare with Fig. 1, A–E. Note that each artificial morph contains internal variation; as discussed in the text, some artificial morphs are circumscribed more broadly in terms of actual achene variation, than others. Morphs are in a proposed order of complexity of wing and wing-tip features. Scale in mm is shown with morph 15.

1. Achenes with no wings, no wing-tips; *Wiggins 12352* (DS). 2. No wings, vestigial tips; *Tracy 6684* (UC). 3. Wings vestigial above, no tips; *Raven 10668* (CAS). 4. Wings narrow above, absent below, tips evident; *Eastwood 143* (UC). 5. Wings extremely narrow, tips vestigial to evident; *Linsdale s.n.* (CAS). 6. Wings to 0.25 mm wide, tips longer than in #5; *Raven 6933* (CAS). 7. Wings wider above, smoothly curving to narrow below, or slightly lobed below; *Howell 41480* (CAS). 8. Wings of medium width, about halfway (ca. 0.75 mm wide) between narrow (#5) and wide (#9, 10, and beyond) with many edge and tip variations. May be incurved below; *Eastwood and Howell 2561* (CAS). 9. Wings 1 mm or more wide, rounded, tips long with a number of variations; *Lee and Mason 9105* (UC). 10. Wings wide, more or less rounded with many edge and tip variations; *Howell 42163* (CAS). 11. Wings wide above, narrower below, with the upper lobes curving into the lower, but the lower not protruding beyond the edge line once it is vertical such that a sinus is not formed; *Howell 29811c* (CAS). 12. Wings wide above, curving to small sinuses below, blending into small lobes that protrude below these, the lobes not as wide as the wings above; *Jepson 18856* (JEPS). 13. Wings wide above and about the same below, divided by a sinus that is wide and fairly deep. Contour of upper and lower lobes more or less continuous; many edge and tip variations; *Raven 6624* (CAS). 14. Wings wide above, about the same or less below, divided by a relatively narrow sinus that is quite deep. Contour of upper and lower lobes more or less continuous; *Jepson 18018* (JEPS). 15. Wings wide, upper lobes wider than the lower, divided by a deep sinus, entire achene rather arrowhead-shaped, the contour of upper and lower lobes not continuous; *Hoover 1996* (JEPS).

lections that exhibited different morphologies [e.g., *Ashwin 535* (CAS), *Howell 45554* (CAS), *Jepson 11563* (JEPS), *Ray 33* (DS), and *Thomas 7101* (DS)]. Glabrous achenes are found occasionally throughout the range of wing-character morphology. Degree and distribution of pubescence also varies over that range. *Howell 45554* has both pubescent and glabrous achenes, but not on the same plant. Thus, pubescence and wing morphology appear to vary independently. In view of this variability, the distinction between *S. sessilis* and *S. neglecta* is unclear.

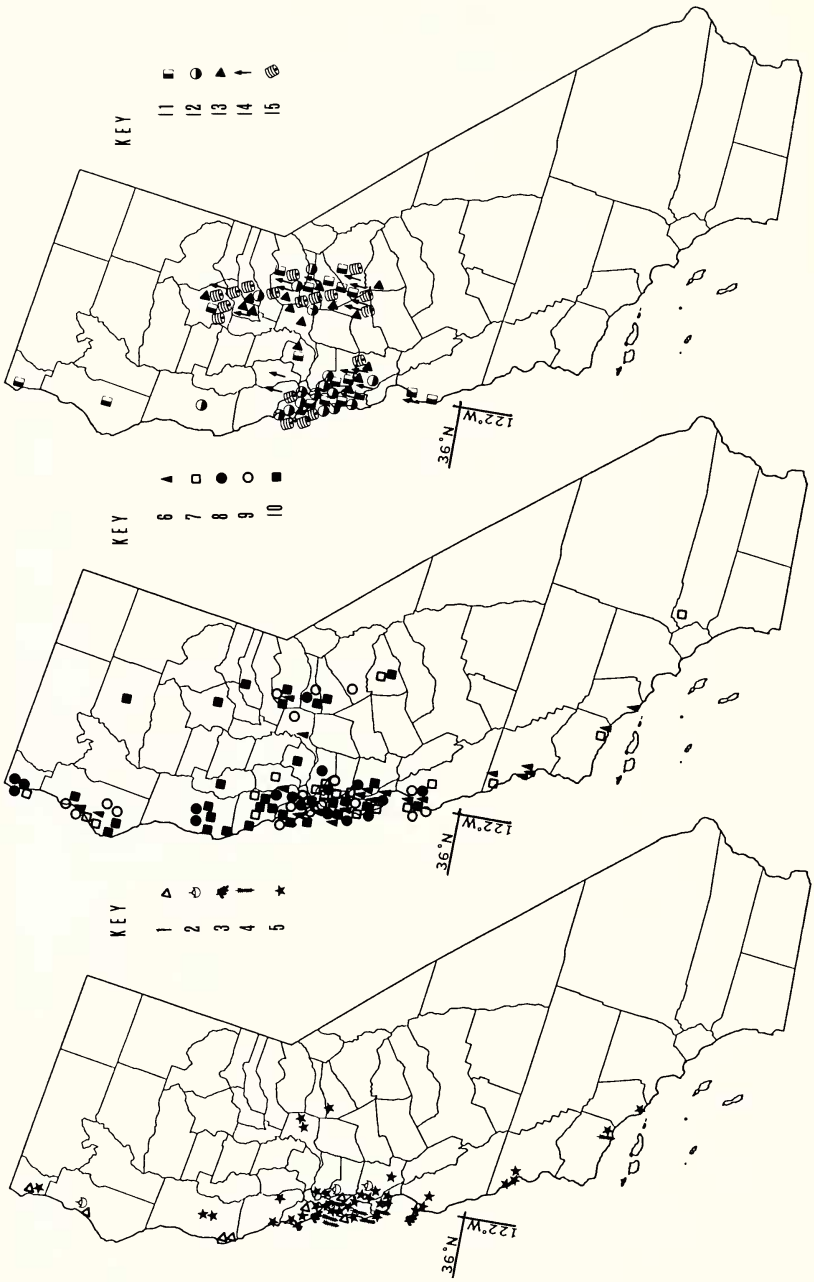
The description of *S. valdiviana* (Philippi 1864–65) includes no specific reference to presence or lack of achenal pubescence, so it corresponds with a number of the specimens examined in this study [e.g., *Ashwin 535* (CAS), *Howell 21653* (CAS), *Koch 812* (UC), *Rose 39154* (UC), *Tracy 6684* (UC), and *Wiggins 12352* (DS, UC)]. Nuttall (1841) described *S. daucifolia* as "slenderly margined" and "minutely bidentate at the summit". Philippi (1864–65) described *S. valdiviana* as "haud alatis" (having no wings) and "spinoso coronatis" (spined crown). Cabrera (1949) includes an illustration of *S. valdiviana* that shows no wing-tips. Because the wings have been an important descriptive character in the literature, the assumption that the term "margin" was used by Nuttall (1841) to refer to the wing is a logical one. The descriptions "slender margin" (i.e., very narrow wings) and "haud alatis" (i.e., lacking the wide wings some other achenes have) are not greatly distinct. The descriptions "minutely bidentate at the summit" and "spinoso coronatis" also are similar; both refer to the small wing-tips that occur in achene morphs 2, 4, and 5 (Fig. 2). Therefore, the original published descriptions for *S. daucifolia* (Nuttall 1841) and *S. valdiviana* (Philippi 1864–65) are similar. Significant variation occurs in wings and wing-tips for artificial morphs 1–5 (Fig. 2), which is the range described for achenes of both *S. daucifolia* and *S. valdiviana.* The distinction between the two taxa is unclear.

The specimens cited by Crampton (1954) to support recognition of *S. daucifolia* differ morphologically from each other and, in some cases, from Nuttall's (1841) description. *Tracy 1089* (UC) has achenes with narrow wings and sinuate edges, often wider above, with long wing-tips; *Rose 39154* (UC) and *Wiggins 12352* (DS, UC) have achenes with no wings and no wing-tips (morph 1, Fig. 2); and *Eastwood 143* (UC) has achenes with the widest portion of the wing above, the wings absent below, and the wing-tips curved sharply inward (obscured behind the stylar spine in Fig. 2). Crampton's (1954) illustration of *Eastwood 143* is similar to achenes I examined, but differs in details of wing morphology. Crampton cited a specimen he called "*Les Koch 812*", which probably corresponds to *Leo F. Koch 812* (UC). Examples of achene morphs 1–10 were found on this sheet. Crampton (1954) provided illustrations of *Crampton 1121*

and *Crampton 1223,* with no discussion of these in the text. On examination, I found achenes from these specimens to correspond loosely with the illustrations, but they differ substantially in detail. Apparently the achenes examined by Crampton (1954) were different from those seen in the present study, which again suggests taxonomic unreliability in achene characters.

Soliva collections that show variation of achene morphology between plants on the same sheet or within individual plants or capitulae are listed below. Each collection is listed with the artificial achene morph numbers (see Fig. 2) corresponding to achenes found on that sheet. An asterisk indicates variation within the same plant: Alameda Co.: *Lee 701* (JEPS), 5, 7, 8. Amador Co.: *Hansen 1054* (UC), 8, 11, 12, 14*. Butte Co.: *Ahart s.n.* (CAS), 10, 14*. Humboldt Co.: *Davy 5684* (UC), 9, 11*. Mendocino Co.: *Koch 812* (UC), 1–10. Monterey Co.: *Howell 41480* (CAS), 6, 7*. San Mateo Co.: *Abrams 2423* (DS), 6, 10, 14; *Dudley s.n.* (RSA), 11, 12*; *Ferris 4157* (DS), 11, 12, 13*; *Ray 37* (DS), 7, 12*; *Ray 38* (DS), 4, 7, 8*; *Ray 40* (DS), 6, 12*, *Thomas 4283* (DS), 4, 7, 8*. Santa Clara Co.: *Dudley s.n.* (DS), 6, 12; *Thomas 4822* (RSA), 8, 11*. Santa Cruz Co.: *Ray 36* (DS), 6, 7*. Sonoma Co.: *Brandegee s.n.* (POM), 5, 10, 14*. Tuolumne Co.: *Howell 40693* (CAS), 14, 15*; *Johannsen 883* (UC), 9, 11, 15*.

Dispersal. Humans appear to be a major factor in the spread of *Soliva* in its role as an adventive species. It consistently occurs in either hard-packed paths, waste ground, dirt roads, or cultivated lawns. In collecting, I observed that achenes easily became imbedded in my hands. Achenes are probably dispersed on shoes or clothes, or on the tires of cars or other machines. It seems likely that in lawns on the Stanford campus, where *Soliva* occurs frequently and is spreading, achenes are moved on the tires of large lawnmowers. To test the hypothesis that achenes can move in tires, I rode a balloon-tired bicycle through some mature patches of *Soliva* in a lawn, and then checked both tires after about 150 m riding distance. Five achenes were found, two of which were firmly imbedded. This indicates that not only can short distance dispersal occur in tires, but also longer distance movement because the firmly imbedded achenes might remain so for some time. *Soliva,* therefore, is a genus well adapted to dispersal within an area in which the plants are already established, and to locations that may be quite remote. Such new locations are generally in well-travelled areas, where the achenes are most likely to become detached from the dispersal agent and to be pressed into the ground by subsequent traffic. The possibility exists that the distribution pattern in well-travelled and populated areas results from sampling. That is not sufficient reason to discredit overall collection evidence because of the additional strong evidence of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achene dispersal adaptations and the many collections from similar microhabitats.

Distribution. Soliva is well established in watered lawns and plantings in many places in California. There are few collections from urban southern California (Los Angeles basin and vicinity), although I have collected *Soliva* in lawns in Santa Monica, Arcadia, Newport Beach, and rural Orange Co., and I have observed it growing in lawns near USC. It is unlikely that the genus is established in many natural or unwatered areas in southern California, because of low seed carryover (Johnson and Lovell 1980) and the relatively long wet period required for growth. In contrast, *Soliva* is probably established in more locations in the San Francisco Bay region and northern California than records indicate.

Distribution maps (Fig. 3) show collection locations for many *Soliva* specimens examined in this study, with a symbol for each indicating an artificial achene morph that corresponded most closely with achenes from that specimen (variation in the same collection not indicated). The three maps are designed to show the distribution of each of the 15 artificial achene morphs. This is necessary because species of *Soliva* have been recognized by alleged localization of particular achene morphologies. Examination of the maps (Fig. 3) may give the impression that achene morphs 11–15 (Fig. 2) occur more often in the Sierra Nevada foothill areas and that morphs 1–6 occur more often on the southern coast. Crampton (1954) made similar observations and used them to support recognition of *Soliva pterosperma* (Sierra foothills) and *Soliva daucifolia* (southern coast). I observed, however, that all achene morphologies were distributed randomly and in high density in the San Francisco Bay region, from which there are more collections than any other region in the state. Also, morphs 5–8 have been collected in the Sierra foothills (Fig. 3). Because of the low frequency of collections in the Sierra foothills and the southern areas (relative to the Bay region), and the random distribution of morphs in the Bay region, localization of particular achene morphologies in the Sierra or southern areas does not seem plausible. Thus, there appears to be no separation of achene morphologies throughout the range of *Soliva* in California.

Conclusion. My observations of achene morphology show that a continuum of variation exists for the achene wing and wing-tip characters in the California collections of *Soliva.* Based on these observations, and the lack of any other consistent variations or major

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FIG. 3. Distribution of *Soliva sessilis* in California. Three maps are provided for clarity in areas of high specimen density. Keys match symbols on maps to artificial achene morph numbers (1–15) in Fig. 2.

separations of habit or habitat, I conclude that only one species of *Soliva* occurs in California. Because this species also occurs in other parts of the world (such as Australia, New Zealand, and South America), and indeed has been introduced into California, this conclusion also applies on a wider basis. By priority of publication, *Soliva sessilis* is the name for this species, and thus the names *S. pterosperma* and *S. daucifolia* are synonyms. The names *S. neglecta* and *S. valdiviana* also appear to be referable to *S. sessilis.*

Taxonomic Treatment

Soliva sessilis Ruiz Lopez & Pavon, Syst. Veg. Fl. Per. Chil. 215. 1798.—Type: Chile, "Habitat in plateis et pratis *Conceptionis* (sic) *Chile,* praesertim ad *Mochita, Hualpen, Andalien* et *Gavilan* tractus"; no specimens seen; description and earlier illustration (Ruiz Lopez & Pavon, Syst. Veg. Fl. Per. Chil. 113, tab. 24, 1794) fix application of the name. See Cabrera (1949) for additional synonymy.

Gymnostyles pterosperma A. L. Juss., Ann. Mus. Natl. Hist. Nat. 4: 262, tab. 61, f. 3. 1804.—*Soliva pterosperma* (A. L. Juss.) Less., Synop. Gen. Compos. 268. 1832.—Type: Argentina, Buenos Aires, "Ex Bonaria. Car. ex sicca in herb. Commers.", no specimens seen; illustration fixes application of the name. See Cabrera (1949) for additional synonymy.

Soliva daucifolia Nutt., Trans. Amer. Philos. Soc., ser. 2. 7:403. 1841.—Type: California, ". . . within the limits, and in the immediate vicinity of St. Barbara"; no specimens seen; description allows certain application of the name.

Soliva valdiviana Philippi, Linnaea 33:168. 1864–65.—Type: Chile, "Frequens in prov. Valdivia"; no specimens seen; description allows certain application of the name.

Soliva neglecta Cabrera, Notas Mus. La Plata 14:128. 1949.—Type: Argentina, Jujuy, Santa Ana, 3100 m, 29 Feb 1940, *A. Burkart and N. S. Troncoso 11665* (LP; isotype: SI) (not available).

Herbaceous annuals with fibrous roots. Ascending, spindly-stemmed plants to nearly acaulescent plants, or clumpy and compact plants with glomerate leaves and capitulae, or spreading plants with decumbent to prostrate stems and elongate internodes. Compact plants 2–7 cm tall, spreading plants 25 cm diam. Stems 1–10 from base, light- to dark-colored, often purple-spotted, sparsely pubescent to villous. Leaves to 5 cm long, petioled, the bases broad, ± clasping; once-pinnate, the pinnae with 2–8 ± palmate narrowly lanceolate lobes, often one lobe smaller, the terminal pinna sometimes single; puberulent to sericeous or villous. Capitulae sessile in axils; disciform; receptacle convex or low-conic; involucre of 5–12 subequal phyllaries, broadly ovate to lanceolate, abruptly acute, in 1–2 series,

2–3 mm long, green to hyaline, pubescent to villous; disc flowers 4–6, perfect, minute, greenish-translucent (yellow stamens within), 4-merous, probably functionally staminate, surrounded by 10–12 naked pistillate flowers. Achenes 3.5–5.2 mm long including stylar spine, the ovate to lanceolate central body ± carinate, style persistent, becoming hard and sharp, stigmas persistent or deciduous. Achenes wingless (with or without toothlike wing-tips) to wide-winged, the wings thin, opaque to regionally hyaline, the edges notched, incurved, split, cracked, or sinuate; the wing-tips from short, blunt, toothlike projections to long curving tips with thin edges; achenes light green to dark brown, often with minute purple spots, glabrous to variously pubescent. Probably self-fertile. Feb–Jul. Disturbed, hard-packed and weedy areas that receive sufficient water for seed set, especially paths, dirt roads, roadsides, and other well-travelled areas; also in watered lawns.

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Literature Cited

Cabrera, A. L. 1949. Sinopsis del genero *Soliva* (Compositae). Notas Mus. La Plata, Bot. 14:123–139.

Crampton, B. 1954. Observations on the genus *Soliva* in California. Leafl. W. Bot. 7:196–198.

Healy, A. J. 1953. Contributions to a knowledge of the naturalized flora of New Zealand No. 3. Trans. Roy. Soc. New Zealand 81:23–26.

Johnson, C. D. and P. H. Lovell. 1980. Germination, establishment and spread of *Soliva valdiviana*. New Zealand J. Bot. 18:487–493.

Munz, P. A. 1959. A California flora. Univ. California Press, Berkeley.

Nuttall, T. 1841. Descriptions of new species and genera of plants in the natural order of the Compositae. Trans. Amer. Philos. Soc. (New Series) 7:403.

Philippi, R. A. 1864–65. Plantarum novarum Chilensium. Linnaea 33:168–169.

Raven, P. H. 1963. Amphitropical relationships in the floras of North and South America. Quart. Rev. Biol. 38:151–177.

Ray, M. F. 1984. The genus *Soliva* (Asteraceae) in California. M.S. thesis, Stanford Univ., Stanford, CA.

Voss, E. G. et al. 1983. International Code of Botanical Nomenclature, adopted by 13th International Botanical Congress, Sydney. Regnum Vegetabile 111.

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